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Quantifying predation on Baltic cod early life stages

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Abstract

Predation on cod eggs by sprat and herring is known to be one of the processes influencing reproductive success of the Eastern Baltic cod, and has been reported to have contributed to lack of recovery of the stock in the 1990s. This study quantifies the predation on cod eggs in the Bornholm Basin, the major spawning area of cod in the central Baltic Sea, in the 1990's in comparison to the second half of the 2000s. The analyses involve estimating daily consumption rates of predator populations, which are then compared with corresponding daily egg production rates. As a methodological advancement compared to earlier studies, spatially resolved information on predator distribution and abundance is utilized in quantifying predator stock size. This resulted in more realistic consumption estimates in relation to overall egg production, compared to earlier studies that consistently overestimated predation pressure by clupeids. Our results suggest a generally lower predation pressure on cod eggs in the mid- to late-2000s, due to a combination of reduced predator abundance and lower daily rations by individual predators.

Keywords: Baltic Sea, Atlantic cod, sprat, herring, egg production, egg consumption, recruitment

Introduction

In the Baltic Sea, cod (*Gadus morhua* L.) is the main predator fish (Sparholt 1994), being both of high ecological and commercial importance (e.g., Rudstam et al. 1994, Kornilovs et al. 2001). The eastern Baltic cod was in a depleted state in the 1990s-early 2000s, due to a combination of high fishing intensity and reproductive failure (Bagge et al. 1994, Köster et al. 2003, MacKenzie et al. 2000). At the same time, the Baltic sprat (*Sprattus sprattus*) population was record high, due to low predation pressure from cod and favourable environmental conditions for reproduction (e.g. Köster et al. 2003). In the Baltic Sea, sprat and herring (*Clupea harengus*) prey on cod eggs, and egg predation was considered as one of the factors limiting cod reproductive success in the 1990s (Köster et al. 2005). Trophodynamic control of recruitment success of a predator species by forage fish has been observed also in other areas. Especially in strongly stratified estuarine systems, pelagic early life stages dwell in intermediate water layers utilized by pelagic fish for foraging. Examples are the Black Sea (Prodanov et al. 1997) as well as the southern (Swain and Sinclair 2000) and northern Gulf of St. Lawrence (Savenkoff et al. 2004).

Quantifying predation pressure exerted by pelagic fish on early life stages has proven to be extremely difficult (Bailey and Houde 1989, Heath 1992). The studies on this topic are scarce (Houde 2008), despite the general advancements in observation technology and ecosystem understanding. Predation on early life stages is also highly variable; in the Baltic Sea depending, amongst others, on hydrographical conditions (Köster et al.

2000 and et al. 2011). Challenges in quantifying egg predation are apparent also in the Baltic Sea, as the magnitude of daily cod egg consumption has consistently been estimated to be higher than production. Thus, the results have only been used as relative predation indices in modelling studies (Köster et al. 2005, 2009). The largest source of uncertainty was introduced by estimates of the predator population size in cod spawning areas at spawning time (Köster et al. 2005). In line with this observation, Paradis et al. (1996) concluded that it will be essential to study factors that influence the timing of encounters between early life stages of fish and potential predators. Accordingly, quantifying effective predator population size is the major methodological focus of the present study.

The aim of the present study is to quantify cod egg predation by sprat and herring in the Bornholm Basin, i.e. the main cod spawning area in the Baltic Sea (Köster et al. 2009). Köster and Möllmann (2000) have estimated cod egg consumption rates in the late 1980s until the mid-1990s. Since then, several ecological changes have taken place in the Baltic Sea, which can be expected to have impacted on egg predation, such as expanded spawning season of cod (Neumann et al. 2014) and changed predator distribution (Casini et al. 2004). Furthermore, the eastern Baltic cod stock has been estimated to have increased in the second half of the 2000s (ICES 2016) which has been associated with improved recruitment (Eero et al. 2012a, 2015), despite pertaining adverse environmental conditions for cod in the Baltic Sea. This calls for updated information on the major processes acting on cod recruitment, including predation pressure. In this study we estimate cod eggs predation in 2004-2008 and compare this

with updated estimates from the 1990s to elucidate potential changes in predation mortality on cod eggs. In this respect, the present study is a follow-up to Neumann et al. (2014) that demonstrated changes in the diet composition of sprat and herring in 2004-2008 compared to the 1990s. In our investigation, we use this information to quantify predation pressure on cod eggs, with major focus on methodological improvements of calculation procedures compared to earlier studies, such as quantifying the effective predator stock size. Our study contributes new quantitative knowledge on one of the key processes governing cod recruitment in the Baltic Sea and provides both ecological and methodological input to similar investigations elsewhere.

Materials and Methods

Data

The analyses combine i) diet composition data of sprat and herring, ii) hydrographic measurements and gastric evacuation modelling to estimate the daily cod egg consumption by individual predators, iii) stock assessment model output and hydroacoustic surveys to derive spatially-resolved predator abundances and iv) cod egg abundances and production rates from ichthyoplankton surveys conducted concurrently to the stomach sampling. The data sources and calculation procedures are described in detail below.

Field sampling

Data on diet composition of sprat and herring, cod egg abundance and vertical distribution, hydrographic conditions and clupeid abundances were collected during

standard hydrography/ichthyoplankton and trawl/hydroacoustic surveys in the Bornholm Basin by German RV “Alkor” in 2004-2008. Corresponding data from 1990-1999 were available from earlier studies (Köster and Möllmann 2000; STORE 2003). Sampling was conducted in the Bornholm Basin (Fig. 1) twice a year in May/June and July/August, further referred to as spring and summer, respectively.

Sprat and herring were collected for diet composition analyses deploying an “Engel Kombitrawl (KT) or an “Engel Young Fish Trawl” (YFT) (see also Neumann et al. 2014). Fishery hauls were conducted either on or near stations from the regular ichthyoplankton station grid (see below) or on north-south transects through the Bornholm Basin. Fishery operations were conducted during day time, i.e. the feeding period of both species (Köster and Schnack 1994). Trawl hauls were targeting fish aggregations identified by a ship-mounted Simrad EK 60 scientific echosounder and performed with a general duration of 30-minutes at a speed of ca. 3 knots. Sprat and herring stomachs were taken by 1 and 2 cm fish length-classes, respectively and immediately after weighting and measuring the fish and the stomachs were dissected and preserved in borax-buffered 4% formaldehyde-seawater solution.

In the lab, the wet weight of stomach contents was estimated as difference between full and emptied stomach. The stomach contents were transferred into sorting solution (Steedman 1976) and were later analysed to major taxonomic groups using an identification key by Kazanova (1953). The handling of stomachs followed the same standardized procedure described in Köster (1994) and Köster and Schnack (1994).

Hydroacoustic data were recorded continuously during survey operations with a hull-mounted Simrad EK 60 scientific echosounder operated at 38 kHz at a ship speed of ~10 knots, after a standardized calibration of hydroacoustic equipment prior to survey operations (Foote et al. 1986). Clupeid school echoes were identified and integrated using Echoview software (with an implemented school-detection algorithm (Echoview Software Pty Ltd 2015). School detection parameters were set according to Nilsson et al. (2003) and implemented on daytime data, taking diurnal vertical migration into account.

Ichthyoplankton samples were collected on a regular station grid (on average 33 stations per cruise, with ~9 nmi distance, Fig. 1) covered with double-oblique hauls using a Bongo net (335 to 500 μ m mesh size) from the surface to ~3 m above the bottom, following procedures described by Wieland (1988). For the estimation of cod egg abundances, only stations within the 60m depths contour were utilised (defined as Bornholm Basin). This area was consistently covered over the entire time series and contains the vast majority of the egg production by the stock (> 95%; Wieland and Jarre, 1997). Data on the vertical distribution of cod eggs originate from a Hydrobios multi-opening and –closing net consisting of 9 nets (335 μ m mesh size), deployed at a towing speed of 3 knots. Two (spring 2006) or three vertical profiles were sampled per cruise (Fig. 1). Bongo and multinet samples were preserved in 4% borax-buffered formaldehyde seawater solution. Fish eggs were identified from subsamples to species level and development stage (Kazanova 1953) (min. 100 eggs per station) and risen to the total sample volume. The volume of filtered water and water depth per station were

used to calculate the total cod egg abundance ($n\ m^{-2}$). To estimate vertical fish egg distribution, the volume of filtered water per depth stratum was utilised to compute densities ($n\ m^{-3}$).

Diet composition and ichthyoplankton sampling, data processing and analyses in the 1990s and in 2000s followed similar procedures and are therefore directly comparable.

Daily consumption of predators

To estimate the amount of the daily food intake by individual herring and sprat an exponential form of the general model of gastric evacuation was applied according to the procedure used by Köster and Möllmann (2000) which incorporates the actual ambient temperature as a variable and considers the type of food (Temming 1996, see also Möllmann and Köster, 1999)

$$S_t = S_0 \times e^{-R' \times t \times e^{A \times C}}$$

with: S: stomach contents in terms of wet weight (g), R': food type constant, A: temperature coefficient, C: ambient temperature (°C) and t: time interval. This function was fitted to median stomach contents as well as to corresponding 25th and 75th percentiles derived from 24-h fisheries and deck tank experiments performed in the Bornholm Basin (STORE 2003, Temming 1996). The determined values for the food type constant and the temperature coefficient were 0.084 and 0.129 for herring and 0.108 and 0.073 for sprat, respectively.

Following a procedure suggested by Pennington (1985) the average individual daily ration (F_T) of individual herring and sprat was estimated by:

$$F_T = R' \times S \times T \times e^{A \times C} + S_t - S_0$$

with T: duration of the daily feeding period of sprat and herring (hours of daylight; Köster and Schnack 1994, Fetter and Davidjuka 1996) and S_t and S_0 : the average stomach content at the end and the beginning of the feeding period, respectively (Köster 1994).

Average ambient temperatures (C) in the area of 60-80 m water depth collected on the station grid during the ichthyoplankton/hydrographic surveys (Fig. 1) with a vertically deployed CTD-ADM probe were used or (in case of missing values) the data were derived from the ICES Oceanographic Database. S_t and S_0 were calculated as mean relative deviations from the average stomach content during daytime, 2 h after sunrise and 2 h before sunset, when food ingestion commenced and stopped (Köster 1994).

The daily ration of fish eggs was derived assuming the same ratio between daily food intake and

average stomach content for eggs in numbers as for daily food intake and total food in weight. Finally, the daily ration of cod eggs ingested was calculated by partitioning the daily ration of all fish eggs according to the determined species composition. Generally, all unidentified fish eggs found in the stomachs could be raised to the proportions of identified eggs with an exception of sprat diet composition in spring 2005 and 2008. Therefore, for these dates, daily rations of unidentified fish eggs were provided.

Predator distribution and abundance

The effective predator abundance was considered to be represented by sprat and herring abundances within the time and area of cod spawning. The cod spawning area was defined as the area in the Bornholm Basin with water depths of 60 m and deeper (Wieland 1988). The official stock assessments of sprat and herring cover larger areas in the Baltic Sea and thus had to be downscaled to obtain the estimates of effective predator abundances (see Fig. 2). The downscaling followed two steps. At first, we derived abundance estimates of sprat and herring in ICES Subdivision (SD) 25 on quarterly basis (mid May and mid July) from area-disaggregated multi-species SMS model runs (Eero et al. 2012b). SD25 includes the defined spawning area of cod, however also adjacent areas. Therefore, in a second step the estimates for SD25 had to be further downscaled. This was done using both data and results of ICES coordinated hydroacoustic surveys as well as hydroacoustic measurements conducted during the stomach sampling/ichthyoplankton/hydrographic surveys that when combined allowed

estimating relative abundances in- and outside the defined spawning area within SD25
(see Table S1¹).

Horizontal distribution and abundance

To derive horizontal distribution and abundance indices of both sprat and herring in
spring, hydroacoustic data from the Baltic International Acoustic Spring Survey (BASS)
were used. Aggregated and binned (1 nmi interval) NASC (Nautical Area Scattering
Coefficient, $\text{m}^2\text{nmi}^{-2}$) data were available including geographical position and mean
water depth of each interval. Based on mean geographical position, each data point
was allocated to an ICES rectangle and a corresponding mean bottom depth. NASC
values representing an index of abundance were split and dis-aggregated into species
(herring, sprat and cod) based on catch per unit of effort (CPUE) and length frequency
data from corresponding trawl hauls conducted in the corresponding rectangle
(according to Simmonds and MacLennan 2005). The total species-specific NASC then
was partitioned into areas outside and inside the Bornholm Basin (i.e. water depth ≥ 60
m), yielding relative distributions of both herring and sprat for the corresponding areas.
As no BASS data were available for the period 1990-1998, species specific averages
for the ratio outside-inside were derived from the later years covered.

Distribution and abundance indices of clupeids in summer were derived from the Baltic
International Acoustic Autumn Surveys (BIAS), assuming that distribution patterns in
September/October are also representative for clupeid distribution in summer after

¹ Table S1 with underlying data from figures is available in supplementary.

finalization of spawning (Aro 1989). Contrary to the BASS spring surveys, NASC data were not available for BIAS. Instead, evaluated, ICES rectangle based, species-specific abundance indices were derived from annual survey reports (ICES Planning Group for the Hydroacoustic Surveys in the Baltic, ICES 1990-1995; Baltic International Fish Survey Working Group, ICES 1996-2009, Reports available from <http://www.ices.dk/community/groups/Pages/WGBIFS.aspx>). Species specific abundance indices (per nmi²) were derived for all rectangles within SD 25 and weighed with the size of the area with water depths ≥ 60 m within each rectangle. As with the spring data, distribution and abundance data then were combined to partition the total abundance index for SD 25 into areas in- and outside the Bornholm Basin yielding relative distributions of both herring and sprat for the corresponding areas. As the BIAS survey coverage was either unavailable or considered insufficient in the years 1990, 1993 and 1997, average abundance indices for these years were derived from preceding and subsequent years.

Vertical distribution

As consumption estimates are highly influenced by predator-prey overlap, only predators within the Bornholm Basin (see above) were considered that during their daily feeding period (e.g. Köster and Schnack 1994) actually were dwelling in water layers where cod egg predation can occur (≥ 50 m, see Neumann et al. 2014). As the spatial and temporal coverage of the ICES coordinated surveys was considered too low to derive representative vertical distributions of clupeids within the Bornholm Basin,

hydroacoustic data measured during the stomach sampling surveys (see above) were used. The relative distribution of clupeid NASC values from those surveys recorded during daytime (the daily feeding period of clupeids) was partitioned and aggregated into layers above and below 50 m depth. To estimate the actual fraction of predators overlapping with eggs, the ratio of clupeids below 50 m depth was applied to the relative proportion of herring and sprat within the Bornholm Basin generated from horizontal distribution data. As highly resolved vertical distribution data was only available for the years 2004-2008, the average fraction of clupeids distributed in deeper layers in these years was applied to calculate corresponding abundances for the preceding years.

Total Predator abundance

Obtained fractions of herring and sprat in- and outside of the cod spawning area within SD 25 were utilized to downscale abundance of age 2+ sprat and herring in the entire SD 25 (from stock assessment model) to the actual cod spawning area delineated by the 60 m isobaths. In spring 1995 and 2004, considerable numbers (> 10% of total abundance) of age 1 sprat were encountered in the central Bornholm Basin during the stomach sampling surveys. Accordingly, in these seasons/years, sprat age 1 abundance was also included in the calculation of total predator abundance to account for that observation.

Cod egg abundance and production

Average stage-specific cod egg abundances from stomach samples were standardized to spatial densities ($n\ m^{-2}$) and raised to the area enclosed by the 60 m depth contour (11850 km^2). Dead cod eggs were included in abundances estimates, since dead and live eggs cannot be distinguished in predator gastric contents.

The daily cod egg production was calculated by dividing the average stage-specific abundances of egg stage IA by the development time of the egg stage. The latter is dependent on ambient temperatures (Wieland et al. 2000a), which were derived from hydrographic measurements taken during the vertically resolved ichthyoplankton sampling (according to Wieland and Jarre, 1997). In cases where this was not available, average temperature at 60-80m depths derived from the ICES oceanographic database for May/June and July/August were applied. This water layer consistently contained $\geq 95\%$ of all cod eggs in vertically resolved ichthyoplankton sampling (Wieland and Jarre 1997). Egg mortalities from stage IA to IB were calculated for each survey according to Wieland (1988) and results were then averaged over the time period 1990-2008 to correct the daily egg production estimates for egg mortality within half stage duration time of egg stage IA. Similar to the egg abundance, the corresponding proportion on dead eggs per stage were added to the resulting egg production estimates.

Results

Daily food rations of herring and sprat

The daily food ration of individual herring was on average higher in spring than in summer (Table 1), being similar in the 1990s and in the 2000s. In 2000s spring

sampling dates, the daily ration of fish eggs varied from below 20 eggs d^{-1} in 2004 and 2005 to a maximum of ~363 fish eggs d^{-1} in 2008. The main fraction of fish eggs were cod (an average of 63%). In contrast, in the 1990s, the daily rations of herring contained on average 34% cod eggs only (Table 1). In summer 2004-2008, the daily ration of fish eggs ranged between ~5 eggs d^{-1} (2008) and ~174 eggs d^{-1} (2007) per herring, with an average of >90% of these being cod eggs. Generally higher quantities of cod eggs were consumed in the 1990s with an average of ~154 cod eggs d^{-1} compared to ~66 cod eggs d^{-1} in the 2000s.

The daily food ration of individual sprat was similar in spring and summer. In spring of the 2000s, overall low amounts of fish eggs were ingested by sprat (~11 eggs d^{-1} on average), however a relatively high proportion of those were cod with a maximum ~23 cod eggs d^{-1} (2007). In the 1990s generally higher numbers of fish eggs (78 eggs d^{-1} on average) were consumed, however with a low proportion of cod eggs (max. 27 cod eggs d^{-1}). Maximum daily rations were encountered early and late in the 1990's and in 2007 (Table 1). In summer, the consumption of cod eggs by individual sprat has always been relatively low (max. 15 cod eggs d^{-1}) with the exception of 1997 (~58 cod eggs d^{-1}).

Predator abundance

The predator abundance in the Bornholm Basin within the cod spawning area was estimated to be well below 50% of the total stock size in SD 25, except spring 2005 with around 60%.

Herring abundance in summer was generally higher in the 1990s ($\sim 300 * 10^6$ on average) compared to the 2000s ($\sim 160 * 10^6$), however with a relative high abundance in 2007 ($\sim 360 * 10^6$). The abundance of sprat in the Bornholm Basin was in most years considerably higher than that of herring (on average 85% and 72% of the total clupeid abundance in spring and summer, respectively) (Fig. 3; Table S1¹). Sprat abundance in spring increased over tenfold from early to mid-1990s, levelling off during the late 1990s and declining in the 2000s to levels similar to the early 1990s. Very low numbers of sprat were encountered in spring 2008 (Fig. 3; Table S1¹), caused by an extraordinary shallow vertical distribution of the fish leading to the bulk of sprat being vertically separated from main cod egg concentrations. Similar temporal dynamics were observed in summer, though with a less pronounced increase in the 1990s. Sprat abundance in the Basin in spring was generally by a factor of ~ 10 higher compared to summer.

Prey abundance

Cod egg abundances have in general been higher in summer than in spring, with the exception of 1991, 1997 and 2008 (Fig. 3; Table S1¹). A distinct peak in cod egg abundance was observed in the mid-1990s, when between ~ 550 and nearly $1000 * 10^9$ cod eggs were recorded in the spawning area, followed by low values in the late 1990s (Fig. 3). In the 2000s, an increase in cod egg abundance was obvious both in spring and summer. In spring, cod egg abundances increased from $\sim 100 * 10^9$ cod eggs in 2004 to over $300 * 10^9$ cod eggs in 2008 and in summer from ~ 150 to $\sim 400 * 10^9$ cod

eggs in 2006 with a slightly decrease to below 300 cod * 10⁹ eggs in 2008 (Fig. 3; Table S1¹).

Cod egg predation

In general, with a few exceptions, sprat was the top predator of cod eggs in spring (except 1993, 1994, 2006 and 2008), while herring dominated in summer (except 1997 and 2004) (Fig. 4, Table S1¹). Comparing the daily cod egg consumption rates in the 1990s and 2000s, similar values were estimated for herring in spring, while the consumption in summer was higher in the 1990s.

Sprat on average consumed lower amounts of cod eggs in the 2000s compared to the 1990s, both in spring and summer, but with high variability especially in spring (Fig. 4, Table S1¹).

In terms of overall predation pressure, daily consumption of both predator species combined exceeded the total egg abundance in spring 1992, 1998 and summer 1997 (Table S1¹) and egg production of stage IA in spring 1990-1993, 1997, 1998 and 2004 (Fig. 4; Table S1¹).

In summer, consumption rates were generally lower than production rates, except in 1997 (Fig. 4; Table S1¹). The estimated level of consumption by the clupeid populations in relation to the egg production suggests that predation has been of substantial importance for cod egg mortality especially during spring in the 1990s. Independent of the season, the daily consumption of cod eggs in relation to the daily production was lower in the 2000s than in the 1990s, suggesting reduced predation pressure on cod eggs in later years.

Discussion

Inter-annual and seasonal variability in cod egg predation

The main predatory impact on cod eggs was exerted by sprat in spring and by herring in summer, confirming earlier results by Köster and Möllmann (2000). Predation pressure by clupeids was generally lower in the 2000s than in the 1990s, both in spring and summer. This was related to a combination of lower individual daily rations and reduced abundance of sprat and herring in spring and summer, respectively.

Spatial overlap has been identified as a major factor affecting predation of early life stages by pelagic fish in other sea areas (e.g., Garrison et al. 2000, Hallfredsson and Pedersen 2009). In our investigation, low individual cod egg consumption by herring in summer 2006 and 2008, despite high egg abundances, can be explained by limited vertical overlap, i.e. an unusual situation with herring dwelling shallower than cod eggs during their daily feeding period (Neumann et al. 2014). Similarly, the relatively low consumption by sprat in spring 1993-1995 was associated with a limited vertical overlap between predator and prey; due to improved water conditions in the deep areas after a major salt water inflow in 1993, sprat concentrated deeper than the cod eggs (Köster et al. 2005).

Predation on fish eggs is further affected by the availability of alternative prey with e.g. better visibility (e.g., Sandström 1980, Segers et al. 2007). Herring prefer crustaceans over fish eggs in the North Sea (Daan et al. 1985, Segers et al. 2007) and

macrozooplankton, especially mysids, are the preferred prey in the Baltic Sea when both prey types are available (Köster and Möllmann 2000, Casini et al. 2004). This effect was apparent in our data in summer 2008, when herring preyed intensively on mysids (Neumann et al. 2014), explaining the very low daily ration of cod eggs. Similarly, sprat prefer cladocerans to fish eggs as prey (Köster and Möllmann 2000, Bernreuther et al. 2013, Neumann et al. 2014). The relative warm intermediate water layer observed regularly in summers of the 2000s constituted an ideal habitat for sprat (Stepputtis et al. 2011), which in combination with high abundance of cladocerans in these water layers (Bernreuther et al. 2013) led to a low predation on cod eggs, which were located in deeper water layers.

Apart from the vertical overlap and alternative prey availability, the horizontal overlap between predator and prey further affects the predation pressure exerted by clupeids on cod eggs. While sprat concentrate in the same areas as cod for spawning in spring and early summer, they tend to leave the area after spawning (Aro 1989), which together with changed vertical distribution explains the reduced predation pressure on cod eggs by sprat in summer. In contrast, the abundance of herring in the cod spawning area was low in spring, but increased in summer as spring spawning herring returned from the spawning to their feeding grounds in the Bornholm Basin (Aro 1989). In addition to this meso-scale change in distribution inside and outside of the Bornholm Basin, a large-scale distribution shift from the southern central to the north-eastern areas in the Baltic Sea has been observed for both clupeid species since the early 2000s. This shift is

more pronounced in sprat than in herring with sprat concentrating in the northern Baltic, i.e. outside the cod spawning areas (Casini et al. 2011, Eero et al. 2012b).

Methodological uncertainties in the estimates

Earlier studies calculated cod egg consumption rates by clupeid populations in the central Baltic to be several orders of magnitude higher than the daily egg production rates (Köster and Schnack 2000). Our estimated daily consumption rates also exceeded daily production in a number of occasions, especially in spring. Although this discrepancy is substantially reduced compared to earlier studies, it still indicates either an overestimation of the egg consumption or an underestimation of the egg production. Below we discuss the methodological challenges encountered in the present study.

Firstly, an exponential evacuation model was applied in our study, in agreement with findings of Jobling (1986). However, Bernreuther et al. (2009) found a significant deviation from an exponential function of gastric evacuation curve, resulting in an underestimation of consumption rates at low stomach contents, and an overestimation at high stomach contents, with identical consumption rates for both methods at a stomach content of 3% body weight. In the present study, the stomach contents were on average ca. 1% body weight or lower indicating that the choice of an exponential evacuation model may have underestimated consumption rates, which therefore cannot explain the estimated high consumption rates of cod eggs relative to production. Further, a similar evacuation rate for fish eggs and other prey organisms was assumed. The low proportion of fish eggs identifiable to species level indicates a rapid digestion

beyond identification in sprat, but the remains of eggs can be identified after several hours of digestion, thus being in the order of magnitude determined for mesozooplankton prey (Köster 1994). Therefore, the applied procedure to assume that fish egg shells are evacuated together with other food appears to be more reasonable than to model the digestion rate of fish eggs separately (Köster and Schnack 1994).

Secondly, the estimation of predator abundances within the Bornholm Basin is a source of uncertainty involving two geographical down-scaling steps. Earlier analyses found that sprat abundances estimated directly from hydroacoustic surveys were consistently lower compared to the values from stock assessments after downscaling using relative distribution patterns from hydroacoustic surveys (Köster and Möllmann 2000). This could imply a consistent overestimation of the predator population size (Köster et al. 2005). To explore this effect, alternative predation rates were calculated using predator abundances from hydrographic surveys directly (results not shown), which had a limited effect on inter-annual variability in predation pressure and could not reduce the relatively high consumption rates compared to egg production estimated for spring of the early and late 1990's and 2004. For herring, higher abundances were estimated when using hydroacoustic surveys directly, which would indicate that predation pressure is rather under- than overestimated. Using an average value of the spring fractions of both herring and sprat distributed within the BB in the years 1999-2008 for earlier years with no such distribution data may introduce an error. However, as the overall variance in spatial distribution of both species was low in the years with available data, this error is considered to be of limited concern. Applying acoustic surveys conducted in autumn

to represent relative distribution of clupeids in summer may as well bias the results. Earlier analyses for the 1980s showed that a lower proportion of both herring and sprat was located in the Bornholm Basin in summer than in autumn. However, the encountered deviation was quite limited for herring that is the main predator on cod eggs in summer (Köster 1994).

Finally, in addition to possibly overestimating consumption, the cod egg production may be underestimated. The coverage of the spawning area by the ichthyoplankton station grid is considered sufficient as cod eggs need salinities > 11 PSU to be neutrally buoyant (e.g., Wieland and Jarre 1997). Such conditions only prevail in the central Bornholm Basin that is well covered by the surveys. However, Kraus et al. (2002) obtained by a factor of 2 higher potential egg production estimates based on the abundances of female spawning cod and their fecundity than the egg production values derived from ichthyoplankton surveys. This can be explained by the loss of eggs as a result of atresia, fertilization failure, and mortality during early embryogenesis (Kraus et al. 2002). In our calculations we have taken, in contrast to earlier studies (e.g. Köster and Möllmann 2000, Voss et al. 2011), into account the mortality within egg stage IA, but fertilization success is not considered and it is unclear how fast the non-fertilized eggs are sinking to the bottom.

In conclusion, the cases in which egg consumption rates still exceed production estimates are likely related to an underestimation of the daily egg production, while in

contrast to earlier studies (Köster and Möllmann 2000, Köster et al. 2005) the determination of predation population sizes appears to be substantially improved.

Clupeid predation as a source of mortality on early life stages

Our results confirm that predation on cod eggs by sprat and herring is at times a substantial source of early life stage mortality. Especially during spring, i.e. early in the spawning season of cod, sprat may exert high predation pressure on cod eggs. A gradual shift in peak spawning time in the last decades from spring to summer (Wieland et al. 2000b) has thus decreased cod egg mortality due to predation by clupeids. The lower predation pressure in the 2000s compared to the 1990s was related to generally lower predator population sizes of sprat in spring and herring in summer as well as reduced individual daily egg rations of especially herring in summer. The latter is in line with a limited spatial overlap between predator and prey in the later period (Neumann et al. 2014).

Other potential predators, such as chaetognaths, sticklebacks (Gasterosteidae), moon jellyfish (*Aurelia aurita*) and garfish (*Belone belone*) show only limited horizontal, vertical or temporal overlap with cod eggs. Even if spatial overlap occurs, these predators are either not able to detect or capture the motionless and relatively large eggs (Köster and Schnack 1994, STORE 2003). In later years the ctenophore *Mnemiopsis leidyi* has been suspected to be a substantial predator on cod early life stages. In 2007, *M. leidyi* was highly abundant in the Bornholm Basin with variable inter-seasonal distribution and overlap with cod eggs (Haslob et al. 2007). However, the studies conducted so far did

not find a strong impact on cod egg predation (Schaber et al. 2011, Jaspers et al. 2011). Only scyphomedusae of *Cyanea capillata* have been identified as predators on cod eggs of some importance (Margonski and Horbowa 1996, Barz and Hirche 2005), but their abundances and thus likely also predation rates are comparatively low (Barz et al. 2006).

Clupeid predation on later life stages of cod, i.e. larvae and early juveniles appears to be low as well, caused by a combination of limited vertical overlap and size preferences (Köster and Schnack 1994, Köster and Möllmann 1997). Thus, egg predation by clupeids seems the primary source of early life stage predation mortality.

Predation on fish early life stages has been identified as an issue also in other areas. In the northern Gulf of St. Lawrence a 15-fold decline of cod biomass has been recorded from the mid-1980s to the mid-1990s (Morissette et al. 2003). Similar to the cod stock in the central Baltic, predation on early life stages by pelagic fish is assumed to have a strong negative effect on cod recruitment success (Savenkoff et al. 2004). Field studies to quantify the predation on cod eggs by planktivorous fish have also been conducted in the North Sea and the Lofoten area. In contrast to the Baltic, the impact of egg predation by herring is quite limited in the North Sea (Daan et al. 1985) and low in the Northeast Arctic as well (Melle 1985). This can be explained by a limited vertical overlap between cod eggs and clupeids in these systems during their main daily feeding period compared to the central Baltic Sea and other estuarine sea areas.

In order to assess the relative importance of predation by clupeids for the reproductive success of cod in the central Baltic, other sources of early life stage mortality need to be taken into account as well. Predation on cod eggs will have a limited effect on recruitment if the eggs and later pre-recruit life stages are anyway subject to high mortality due to other reasons such as poor hydrographic ambient conditions for successful egg development (Köster et al. 2005) or insufficient food supply for cod larvae (Hinrichsen et al. 2001).

Especially the lack of oxygen in and below the halocline is a major source of egg mortality in stagnation periods (Plikshs et al. 1993), also affecting larval activity (Rohlf 1999). However, even in a stagnation situation, for example in spring 2002, the daily egg mortality rates due to predation by clupeids were estimated to be higher than mortality rates due to low oxygen concentration (Voss et al. 2011).

An important factor for recruitment success of cod is prey availability for first feeding larvae (Hinrichsen et al. 2002, Möllmann et al. 2005). Huwer et al. (2011) reported a significantly better larval growth in 2007 compared to the mid-1990s, thus larval survival may have improved in the latter half of the 2000s, potentially enhancing recruitment.

Estimating annual variations in recruitment of the eastern Baltic cod in later years is presently hampered by lack of quantitative stock assessment and age information for cod (Eero et al. 2015). However, survey information shows increased abundances of small cod in the mid-late 2000s, which suggest the occurrence of some relatively

stronger year-classes, which have contributed to the observed increase in stock size in the late 2000s (ICES 2016).

Our analyses suggest that predation pressure on early life stages of cod has generally been lower in the 2000s compared to the 1990s, which, in combination with other factors, likely contributed to a relatively higher recruitment, at least in some years. As a next step, dedicated analyses integrating the available information on all major factors influencing cod recruitment would be worthwhile to conduct, to improve our understanding of the relative importance of different processes acting on cod recruitment. Our study contributes to this process with improved and updated quantitative estimates of egg predation. Improved process understanding of recruitment dynamics in the Baltic Sea may also be helpful for interpreting changes in recruitment in comparable systems elsewhere, where similar comprehensive datasets that allow quantifying complex processes like egg predation may not be available.

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Table 1. Average daily ration of individual herring and sprat; ambient temperature [C; °C]; feeding period [T; h], daily rations [FT; gram]; number of fish eggs per stomach (F/st) and daily rations of fish (Feggs) and cod eggs (Fcod; all stages included) in numbers for spring (May/ June) and summer (July/ August) per year and overall mean for the 1990s and 2004-2008. No data available between 2000-2003. * only unidentified eggs.

season	year	month	C	T	FT	herring			sprat			
						F/st	Feggs	Fcod	FT	F/st	Feggs	Fcod
spring	1990	6	6.4	17.1	2.0	11.9	46.1	20.6	0.4	54.8	210.6	15.3
	1991	5	4.9	16.9	1.3	31.5	103.6	29.7	0.4	31.4	110.2	26.5
	1992	5	5.7	16.4	1.2	3.1	10.9	0.0	0.3	46.9	167.9	5.9
	1993	5	4.5	16.7	1.1	14.4	45.0	26.2	0.4	2.1	7.2	4.2
	1994	6	3.8	17.1	1.3	16.5	49.1	44.0	0.4	11.2	37.5	4.2
	1995	5	5.6	16.3	1.6	5.8	20.0	7.4	0.2	8.0	28.3	1.0
	1996	5	3.5	16.4	1.0	5.0	13.8	4.8	0.3	3.3	10.5	2.0
	1997	5/6	5.3	16.9	1.1	44.4	153.1	26.2	0.3	27.3	98.0	20.2
	1998	5	7.5	16.4	1.0	2.6	10.8	1.1	0.3	17.6	69.6	22.2
	1999	5	6.6	16.4	2.6	2.9	11.0	1.7	0.5	9.9	37.4	0.6
<i>average</i>						27.4	100.9	81.9	0.3	2.7	10.8	7.6
	2004	6	4.8	16.6	1.0	5.1	17.1	10.5	0.1	1.2	5.8	5.7
	2005	5	5.7	16.5	1.5	2.1	7.3	2.8	0.3	1.0	3.9*	0.0*
	2006	6	5.6	16.8	1.6	12.3	46.7	33.1	0.3	2.8	13.4	9.5
	2007	5	5.6	16.5	2.0	14.2	70.6	39.7	0.4	5.8	23.6	22.7
	2008	6	4.9	16.7	1.8	103.0	362.6	323.5	0.3	2.5	7.6*	0.0*

average							27.4	100.9	81.9	0.3	2.7	10.8	7.6
summer	1991	7/8	5.6	15.9	1.6	13.5	26.9	22.5	0.5	13.4	22.7	7.9	
	1994	8	4.3	15.4	0.7	52.1	149.2	145.2	0.3	1.5	4.2	2.8	
	1995	7	5.5	16.4	1.0	42.8	146.3	141.0	0.4	0.0	0.1	0.0	
	1996	7	4.2	16.2	0.7	85.0	251.6	240.9	0.2	5.3	15.7	11.4	
	1997	7	5.6	16.4	1.1	65.6	226.2	220.5	0.5	17.6	57.7	57.9	
average							51.8	160.0	154.0	0.4	7.5	20.1	16.0
	2004	7	5.8	16.1	0.9	16.0	57.4	40.4	0.4	6.5	21.9	15.0	
	2005	7	5.7	15.9	1.3	14.6	88.1	80.9	0.4	2.0	7.5	2.1	
	2006	7	5.6	15.6	0.8	7.6	31.1	30.0	0.5	0.0	0.0	0.0	
	2007	8	6.4	15.3	0.9	46.9	173.9	172.0	0.4	0.2	0.7	0.7	
	2008	8	4.9	13.9	0.8	1.2	4.8	4.8	0.4	0.0	0.0	0.0	
average							17.3	71.1	65.6	0.4	1.7	6.0	3.6

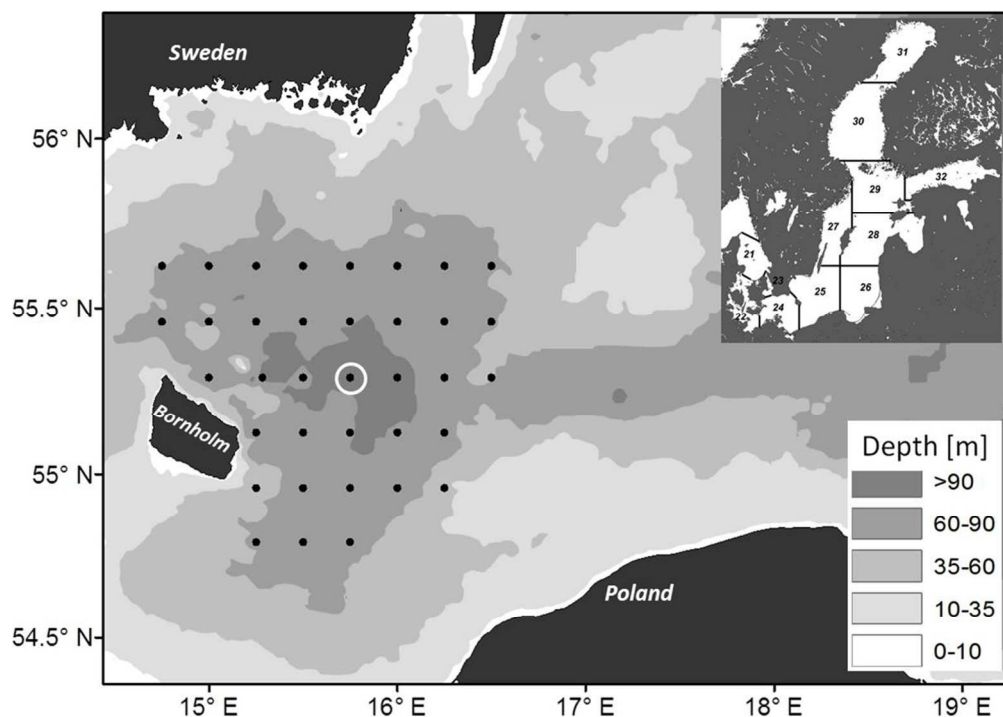


Fig. 1. Investigated area: Bornholm Basin (ICES subdivision 25) in the Baltic Sea (inlet) with the regular Bongo Station grid (black dots) and a Multinet station (circle), sampled between 2004-2008. Fishing was conducted on selected positions on or near stations from the regular grid or in central deep parts of the Bornholm Basin.

203x143mm (150 x 150 DPI)

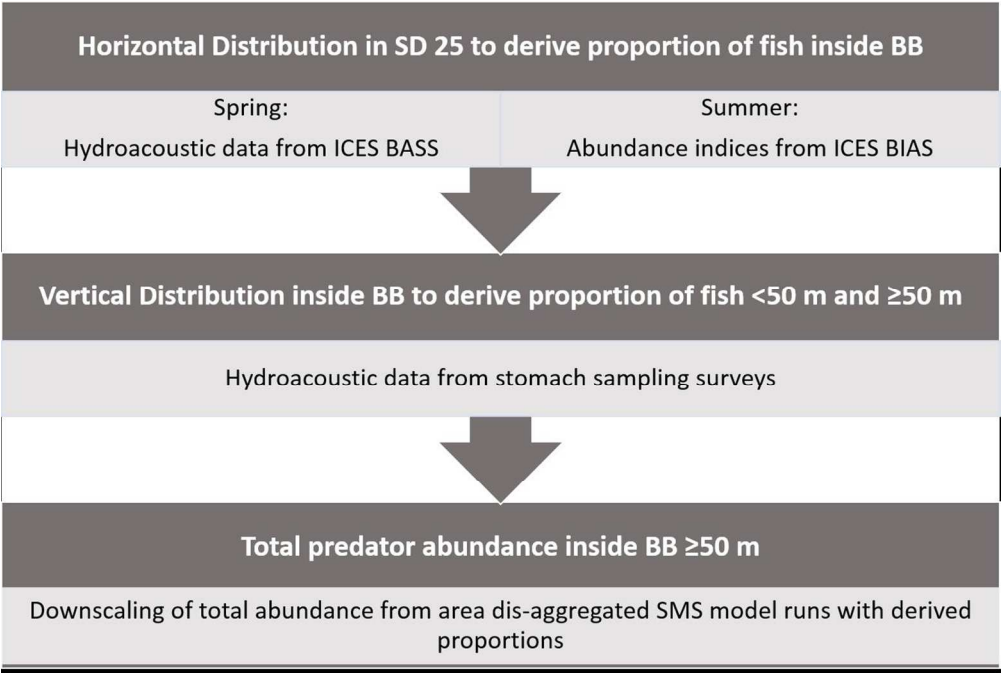


Fig. 2. Data sources and workflow applied to derive estimates of abundance of herring and sprat within layers of cod egg occurrence within the cod spawning area of the Bornholm Basin in ICES Subdivision (SD) 25. BASS – Baltic Acoustic Spring Survey; BIAS – Baltic International Acoustic Autumn Survey; BB – Bornholm Basin.

226x151mm (150 x 150 DPI)

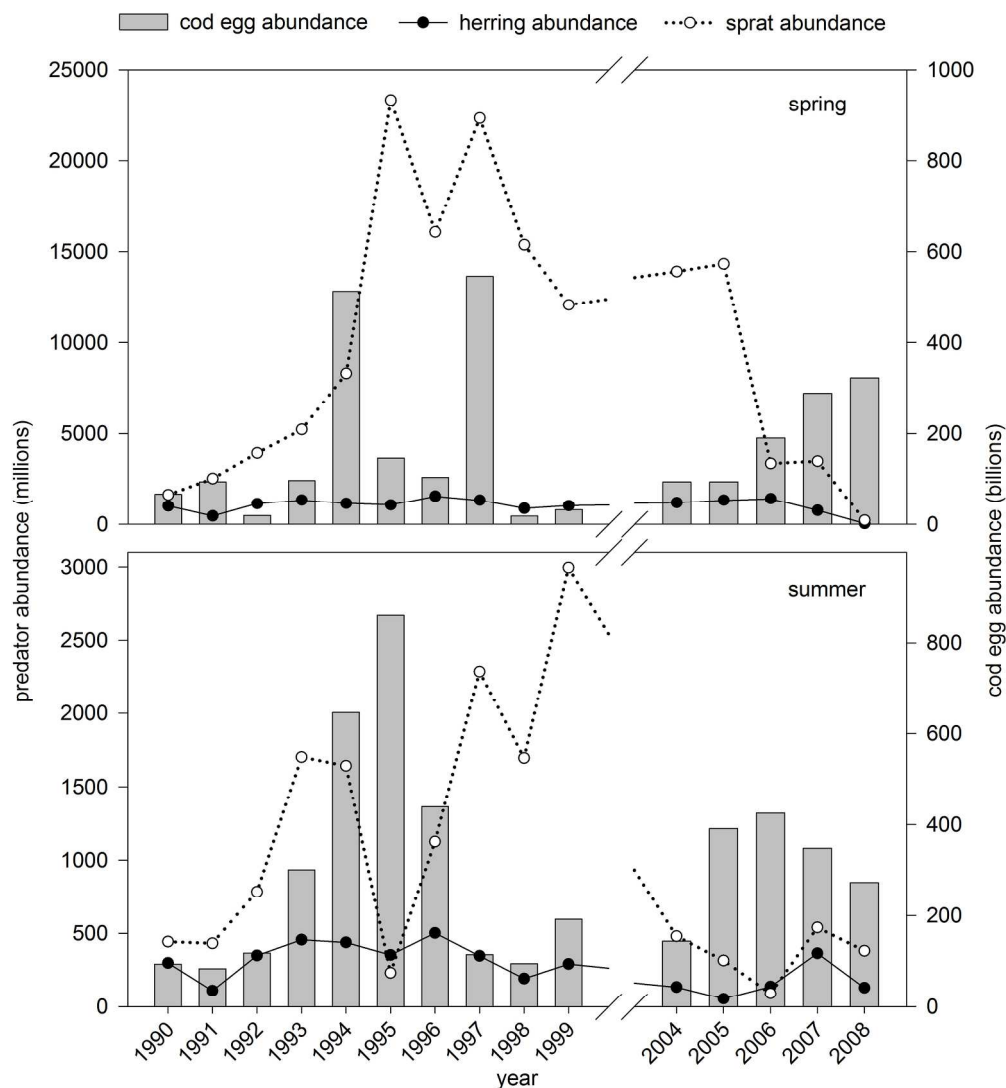


Fig. 3. Abundances of cod eggs (prey) and sprat and herring (predators) in spring (May/June) and summer (July/ August) in the Bornholm Basin. No data available between 2000-2003.

214x232mm (300 x 300 DPI)

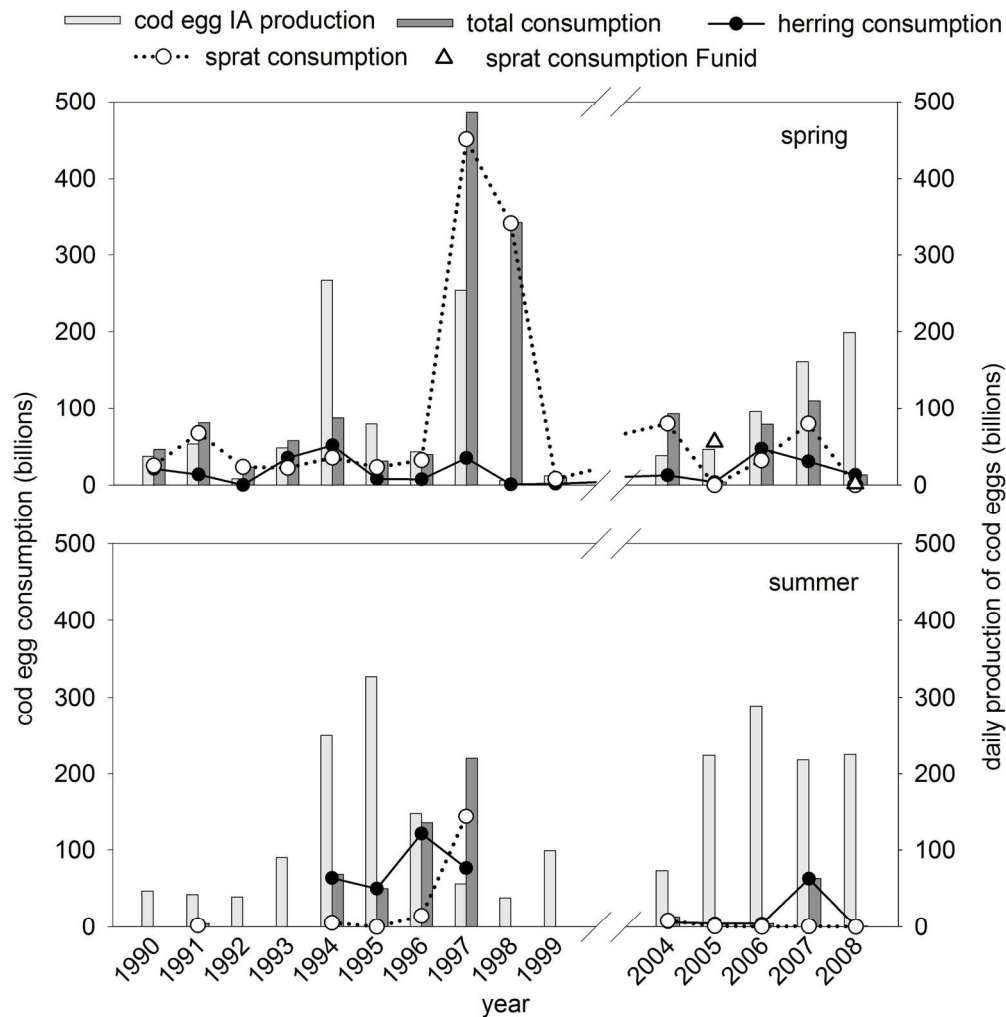


Fig. 4. Cod egg daily production and daily consumption rates, shown separately for sprat and herring populations and combined (clupeids) in the Bornholm. No data available between 2000-2003. Sprat consumption values in spring 2005 and 2008 are based on unidentified fish eggs. No consumption data available: summer 1990, 1992, 1993, 1998 and 1999.

173x176mm (300 x 300 DPI)